CHAPTER 2-5
STREAMS: LIFE AND GROWTH FORMS AND LIFE STRATEGIES

TABLE OF CONTENTS

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Figure 1. ***Fontinalis novae-angliae*** with capsules, exemplifying the **streamer** life form in a mountain stream. Photo by Janice Glime.

Life and Growth Forms

Definitions and Habitats

In bryophytes, **growth forms** are genetically determined forms of adult individual gametophyte plants (Meusel 1935; Mägdefrau 1982). **Life forms** are the environmental expressions of those plants and refer to the growth pattern of the colony. But for many species, perhaps most, a single protonema, developing from a single spore, develops multiple buds that develop into stems and thus form a colony from the onset, giving rise to a **life form** as that colony develops.

A number of bryologists have stressed the importance of life forms as adaptations to habitat conditions. Bryophyte growth forms and life forms can be used to indicate conditions of hydrologic permanence in non-polluted mountain streams (Fritz *et al.* 2009; Vieira *et al*. 2012a). In 165 locations in Portuguese water courses, Vieira *et al*. (2012a) found 11 life forms, with a mean of 2.7 per sample. There was a clear dominance of **smooth mats** (Figure 2; 37%), **tall turfs** (Figure 3; 25%), **fans** (Figure 4; 10%), and **short turfs** (Figure 5; 10%). As habitat zones were less frequently submersed, the number of life forms increased. The deepest or most permanently submersed regions had **mats** and **streamers** [Figure 1; long, dangling stems (Glime 1968)].

Figure 2. ***Frullania tamarisci*** **smooth mat**, a common species near water on canyon walls. Photo by Hermann Schachner, through Creative Commons.

Figure 3. ***Drepanocladus aduncus***, a **tall turf**; this species produces sporophytes when out of water. Photo by Heike Hofmann © swissbryophytes <swissbryophytes.ch>, with permission.

Figure 4. ***Neckera crispa*** **fans**, in this case growing terrestrially. Photo by Malcolm Storey, with online permission.

Figure 5. ***Marsupella emarginata***, an aquatic liverwort that forms a **short turf**. Photo by Hermann Schachner, through Creative Commons.

When Vieira *et al*. (2012b) assessed life forms in mountain streams of Portugal, they found that **thallose liverworts** (Figure 6) typically avoided the flowing water, occurring in shaded locations where they were only seasonally submersed or splashed. These forms were easily damaged by submersion and drag forces. On the other hand, some leafy liverworts that formed **smooth mats** (Figure 2) occurred submersed. Those permanently submersed bryophytes tended to be **streamers** (Figure 1) and **smooth mats**, found up to 30 cm of depth in streams. The **streamers** tended to occur mostly in slower currents of the streambed in full sunlight, whereas **smooth mats** seemed to prefer the torrential water zones in deep shade. Bryophytes subject to frequent water level fluctuations, *i.e.* close to the water, were characterized by a more 3-dimensional life form, but one that was resistant to desiccation and drag forces. These included well anchored **fans** (Figure 4), **dendroids** (Figure 7), and **short turfs** (Figure 5), often occupying vertical surfaces of rocks short distances from the water, but able to benefit from the splash.

Figure 6. ***Pellia epiphylla***, a thallose liverwort that is common on stream banks. Photo by David Holyoak, with permission.

Figure 7. ***Climacium dendroides*** exhibiting the **dendroid** life form. This species can occupy stream banks that get submersed during snowmelt flooding. Photo by Stan Phillips, through public domain.

In the seasonally flooded habitats Vieira *et al*. (2012b) found **tall** and **open turfs** (Figure 8) that have stiff texture, multi-layered tissues, and thick cell walls (Figure 9). These permit them to resist both desiccation and water abrasion. On the upper zones of stones where strong currents are less frequent and in exposed streambeds, bryophytes are represented by **smooth densely-packed cushions** (Figure 10) and **short turfs** (Figure 5) that can resist drought stress (Gimingham & Birse 1957; Muotka & Virtanen 1995; Barrat-Segretain 1996; Vieira *et al*. 2012b). Here and at higher zones on boulders, but in the shade, smooth **mats** (Figure 2) and **fans** (Figure 4) develop (Vieira *et al*. 2012b). Above the level of maximum flooding annuals join the bryophytes, displaying **loose rough mats** (Figure 11) or **wefts** (Figure 12).

Figure 8. ***Tomentypnum nitens***, a wetland **tall turf** species that occurs in fens. Photo by Michael Lüth, with permission.

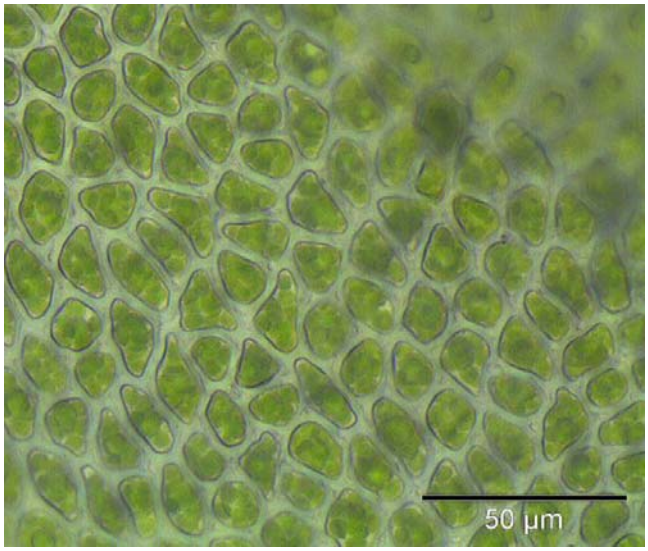

Figure 9. ***Aulacomnium palustre*** leaf lamina showing thick-walled cells. Photo by Kristian Peters through Creative Commons.

Figure 10. ***Andreaea alpina*** **cushion**, a species that can be found on rocks that are occasionally inundated on crags near lakes and streams. Photo by Michael Lüth, with permission.

Figure 11. ***Brachythecium rivulare*** **rough mat**, a species that occurs on stream margins, and in springs and marshes. Photo by Hugues Tinguy, with permission.

Figure 12. ***Trichocolea tomentella*** **wefts**, a species of fens and low areas that can become submersed. Photo by Li Zhang, with permission.

In this same top or higher zones of the boulders, if shaded conditions prevailed for most of the year, **smooth mats** (Figure 2) along with **fans** (Figure 4) developed. Additionally, microhabitats higher than the normal level of maximum floods could be recognized by the co-existence of **annuals** (must grow new plants every year), loose **rough mats** (Figure 11) or **wefts** (Figure 12) that developed mostly associated with deposited sediments.

Birse (1958) related life form to habitat. She found that **wefts** (Figure 12) were typical in freely drained habitats and conditions of intermediate moisture. **Tall turfs** (Figure 3) were more common when water was close to the soil surface. **Wefts** (Figure 12) and **dendroid** (Figure 7) life forms occupied habitats with moisture available from the water table in summer. The semi-aquatic emergents are more likely to be **tall turfs**. Truly aquatic mosses are rarely **tall turfs**, but may be **streamers** (Figure 1, Figure 15), a term introduced by Glime (1968).

Jenkins and Proctor (1985) considered aquatic bryophytes to have two main life forms: **turfs** of densely-set shoots such as those of ***Scapania undulata*** (Figure 13) and ***Hygrohypnum luridum*** (Figure 14) that cling to boulders experiencing turbulent, fast-flowing water; **streamers** (Figure 1, Figure 15) such as ***Fontinalis*** more typical of slower, more streamlined flow. On the other hand, ***F. dalecarlica*** (Figure 15) can occur on boulders in rapids, defending itself with numerous rhizoids and wire-like strong stems.

Thalloid liverworts (Figure 6) grow in zones that are rarely submersed. These liverworts are intolerant of the physiologic stress of continuous submersion or drought and the mechanical stress of mechanical scouring (Gimingham & Birse 1957; Kimmerer & Allen 1982; Martinez-Abaigar & Núñez-Olivera 1991). Rather, they develop in abundance in a more humid and shaded environment above the upper limit of flood-water impact.

Vieira *et al*. (2012b) found that **colonial** growth often occurred through shoot innovations that were firmly attached to the substrate (Figure 16), permitting them to remain in place during heavy flow (During 1990; Grime *et al*. 1990; Muotka & Virtanen 1995). **Ephemeral colonists**, on the other hand, indicate stream zones that are submerged by shifting currents that create abrasive events (Vieira *et al*. 2012b). They survive in tiny rock crevices where they are protected from the torrential currents (Muotka & Virtanen 1995). **Colonists** and **pioneer colonists** are positively correlated with a moderate distance to water and its impact, *i.e.*, in zones that are seasonally flooded with strong discharges (During 1979; Kimmerer & Allen 1982; Vieira *et al*. 2012b). Some **fugitives**, **annual shuttles**, and **stress-tolerant perennials** are able to tolerate slight and infrequent submergence.

Figure 13. ***Scapania undulata***, a **mat**-forming liverwort that can reduce drag in fast water. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Hygrohypnum luridum*** with capsule. Photo by Michael Lüth, with permission.

Figure 15. ***Fontinalis dalecarlica***, a **streamer** species that uses numerous rhizoids to maintain its position in rapid water. Photo by Jean Faubert, with permission.

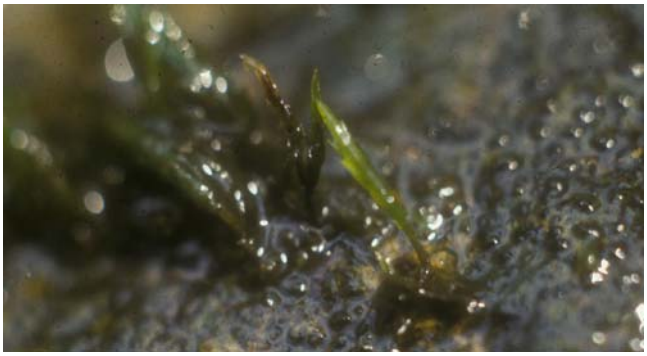

Figure 16. ***Fontinalis novae-angliae*** with new shoots beginning where a stem has been scoured and broken, forming a new colony. Photo by Janice Glime.

Although mountain streams are very different habitats from slow-moving lowland streams, it appears that the life forms defined by Gimingham and Robertson (1950) for English mountain streams can be broadly applied. They identified **large cushions**, **small cushions** (Figure 10), **large turfs** (Figure 3, Figure 8), **small turfs** (Figure 5), **dendroids** (Figure 7), **compact mats** (Figure 2), **thalloid mats** (Figure 6), and **wefts** (Figure 12). As noted, Glime (1968) added **streamers** (Figure 1).

In terrestrial situations, unstable environments are often characterized by acrocarpous mosses such as ***Bryum*** (Figure 17), ***Pottia*** (mostly now in ***Tortula***; Figure 18), and ***Gigaspermum*** (Figure 19) (Ramsay 2006). Pleurocarpous taxa such as ***Hypnum*** (Figure 20) and ***Thuidiopsis*** (Figure 21) seem to require more stable environments. Similar relationships hold in streams, where small, acrocarpous mosses such as ***Blindia acuta*** (Figure 22) live in disturbed areas with movable substrata, whereas the large, pleurocarpous moss ***Fontinalis*** spp. (Figure 23) is characteristic of stable boulders (Muotka & Virtanen 1995). Furthermore, the large **streamers** (***Fontinalis***; Figure 1) occur on the lower parts of stream rocks where they are continuously submersed, whereas the tops of the boulders support growths of low, but not mat-forming, mosses (Virtanen *et al*. 2001).

Figure 17. ***Bryum ruderale***, an **acrocarpous** moss of unstable habitats. Photo by Štěpán Koval, with permission.

Figure 18. ***Tortula lanceolata*** with capsules, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by Michael Lüth, with permission.

Figure 19. ***Gigaspermum repens***, an **acrocarpous** moss suitable for terrestrial unstable environments. Photo by David Tng, with permission.

Figure 20. ***Hypnum chrysogaster***, a **pleurocarpous** moss requiring a stable environment. Photo by Larry Jensen, with permission.

Figure 21. ***Thuidiopsis furfurosa***, a **pleurocarpous** moss requiring a stable environment. Photo by David Tng, with permission.

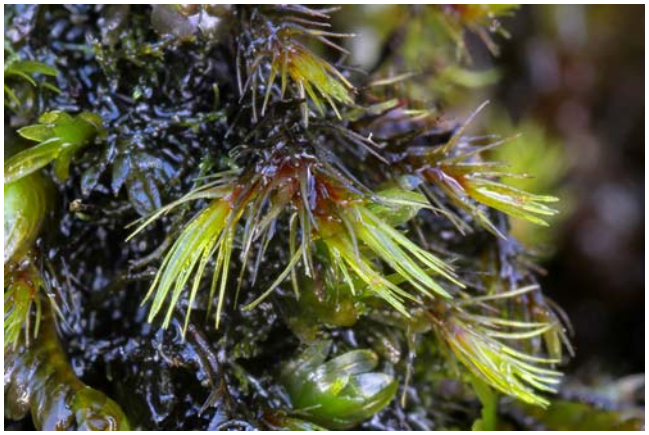

Figure 22. ***Blindia acuta***, an **acrocarpous** species that can live in small crevices in streams. Photo by Barry Stewart, with permission.

Figure 23. ***Fontinalis novae-angliae*** below the water surface and the leafy liverwort ***Plagiochila porelloides*** above. Photo by Janice Glime.

In the Victorian temperate rainforest streams of Australia, all seven of the Gimingham and Robertson (1950) life forms were represented, but not **streamers** (Carrigan 2008), **pendants**, or **tails** (Mägdefrau 1982). However, only two species were of the **cushion** (Figure 10) life form. **Mats** (Figure 2, Figure 11) and **turfs** (Figure 8) were the most represented, with 36 and 32 species, respectively. Wood and sediment had approximately the same distribution of life forms. No life forms stand out on the various sizes of rocks, with approximately the same distribution of life forms on each as for the total set. **Turf** was the only life form that appeared to have significant differences among the rock sizes, with the greatest representation on the medium-sized rocks.

Functional Groups

Monteiro *et al*. (2019) determined the functional structure of bryophytes in headwater streams in Portugal, as represented by life forms. The rock dwellers are typically **rough mats** (Figure 11). Truly aquatic species are mostly perennial, pleurocarpous mosses in **smooth mats** (Figure 24); they rarely produce capsules, and those are typically submerged. The very dynamic mountain flushes, springs, and ephemeral streams support pioneer colonists and **turfs**. Streamsides support **dendroid** (Figure 7) mosses and **thalloid liverwort mats** (Figure 6). At high altitudes, leafy liverworts and competitive perennials predominate. Basic substrates typically have **tufts** and **colonists** of **basophilous** (living or thriving in alkaline habitats) species.

Figure 24. ***Hypnum cupressiforme***, **pleurocarpous** moss forming a **smooth mat**. Photo by Michael Lüth, with permission.

Factors Influencing Life Forms

Life forms are important in determining the drag coefficient and in attenuating the flow velocity, especially within the clump. Dodds and Biggs (2002) showed that even **periphyton** (freshwater organisms attached or clinging to plants and other objects) attenuated the flow velocity with depth. In fact, dense colonies of diatoms (primarily ***Cymbella***; Figure 25) had more effect than did filamentous green algae or red algae. Macrophytes also attenuated the flow rates, but less than the periphyton, and their attenuation was more variable.

Figure 25. ***Cymbella***, a member of the periphyton that can attenuate the flow velocity. Photo by Janice Glime.

One of the factors that influences successful life forms is the **diffusion resistance** to CO_2 uptake. Jenkins and Proctor (1985) measured this resistance in the mat-forming leafy liverworts ***Nardia compressa*** (Figure 26) and ***Scapania undulata*** (Figure 13), both species typical of headwaters. The researchers suggested that the high leaf-area index compensates for the diffusion resistance and permits these mats to effectively exploit low boundary-layer resistance at high velocities while at the same time protecting the liverworts from drag. In the **mats**, boundary-layer resistance limits photosynthesis at flow rates less than ~0.1 m s^{-1}. ***Fontinalis antipyretica*** (Figure 27), on the other hand, is not limited until rates slow to 0.01 m s^{-1}. They attribute this to the **streamer** (Figure 1, Figure 15) life form of ***Fontinalis***.

Figure 26. ***Nardia compressa***, a mat-forming liverwort that can reduce drag. Photo by Barry Stewart, with permission.

Figure 27. ***Fontinalis antipyretica***, having a **streamer** life form that permits it to live in both relatively fast and almost still water. Photo by Hermann Schachner, through Creative Commons.

Proctor (1984) summarized both physiological and structural adaptations of bryophytes for the aquatic habitat. Priddle (1979) reported that bryophytes of still or slow-flowing water had open, slender, elongated life forms. Fast-flowing streams favor tight **mats** (Figure 13) or **cushions** (Figure 10) that mimic or even reduce the drag coefficient of the rocks (Jenkins 1982; Proctor 1984; Jenkins & Proctor 1985). ***Nardia compressa*** (Figure 28) and ***Scapania undulata*** (Figure 29) provide such **compact mats** (Proctor 1984). These two species show reductions in photosynthesis in flow rates below 10 cm s^{-1}; this is most likely due to the need for turbulence to penetrate the spaces between the leaves. But by contrast, as will be seen below, ***Fontinalis*** species typically have trailing shoots (**streamers**; Figure 1, Figure 15) that are able to move easily with the water flow, permitting water to enter the clump. ***Fontinalis antipyretica*** (Figure 30) shows little change in the rate of photosynthesis with flow reduction down to 1 cm s^{-1}.

Figure 28. ***Nardia compressa*** showing **compact mat**. Photo by Hermann Schachner, through Creative Commons.

Figure 29. ***Scapania undulata*** showing **compact mat**. Photo by Michael Kesl, through Creative Commons.

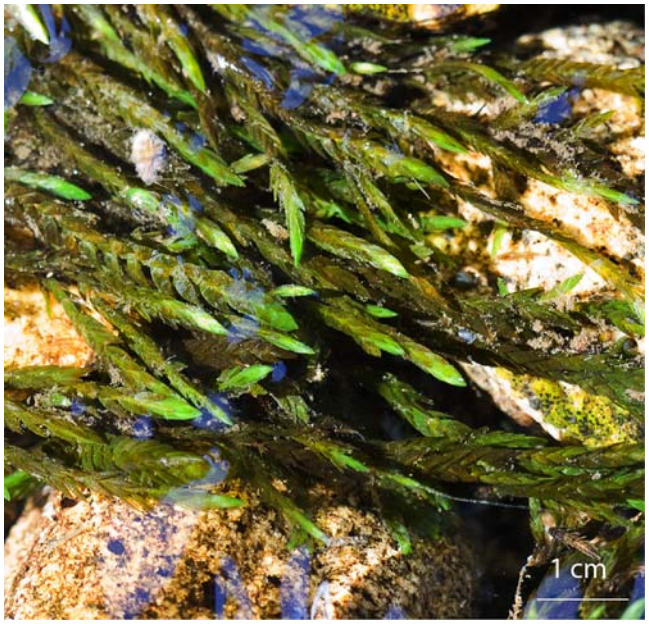

Figure 30. ***Fontinalis antipyretica*** showing a **streamer** life form. Photo from Projecto Musgo, through Creative Commons.

Morphological Plasticity of Life Form

Life forms can differ for a species when its habitats vary. ***Climacium dendroides*** (Figure 31) changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. The Southern Hemisphere species of ***Hypnodendron*** (Figure 32) and ***Hypopterygium*** (Figure 33) behave similarly.

Figure 31. ***Climacium dendroides***, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Li Zhang, with permission.

Bates (1998) reminded us that life forms "minimize evaporative water loss and maximize primary production." Many species show plasticity of life form according to environmental conditions. One of the common characteristics of aquatic bryophytes is the ability to express different life forms when being grown in different conditions. This can be sufficient to cause erroneous descriptions of new species.

Figure 32. ***Hypnodendron menziesii*** from New Zealand, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Jan-Peter Frahm, with permission.

Figure 33. ***Hypopterygium novae-seelandiae***, Saddle Mtn. Rd., NZ, in a genus that changes from an upright **dendroid** plant to a **creeping**, non-dendroid plant after a long submergence. Photo by Janice Glime.

Scapania undulata (Figure 13) occupies a range of habitats from full submersion to rocky ledges in streams of Poland (Samecka-Cymerman 1990). The ledge populations typically are 2-3 cm long, whereas the stream populations are usually 5-10 cm, up to 20 cm. Samecka-Cymerman suggested that low nitrogen might account for the smaller plants on the ledges, a phenomenon known from tracheophytes (Czerwiński (1976; Gumiński 1976). It exhibits a range of morphology that has caused at least one of its forms to be described as separate species (*e.g.* ***Scapania dentata***) (Hiesey 1940), now considered a synonym (Hiesey 1940).

Higuchi *et al*. (2003) reported **mat**-forming green plants from acidic rivers in Japan. When cultured, these produced bryophyte gametophyte buds, indicating that the filaments were protonemata (Figure 34). The large subunit of ribulose-1, 5- bisphosphate carboxylase/oxygenase indicated the moss was 98% similar to ***Dicranella heteromalla*** (Figure 35). This species is common in acidic habitats, including woodland banks, tree stumps, tree roots, hedge banks, dry peaty banks, and sheltered soil of crevices on crags and gullies in the mountains (Royal Botanic Garden, Edinburgh 2019). In Illinois, it occurs also on sandstone walls along streams (Hilty 2017). Its protonemal

growth in the water may be a habitat response that inhibits gametophore development.

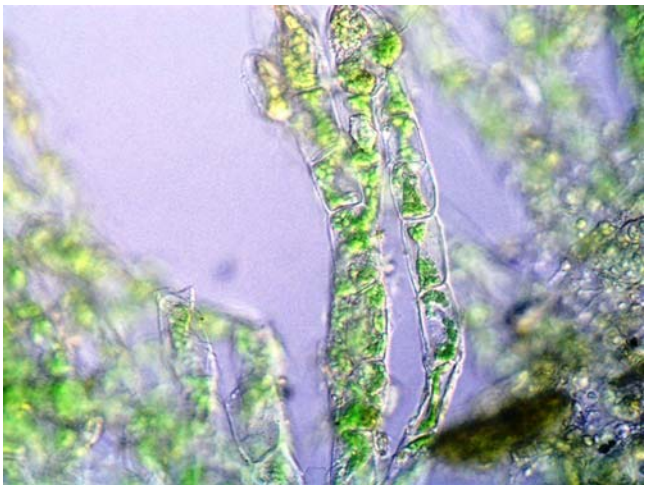

Figure 34. ***Dicranella heteromalla*** protonema, a stage that seems to stop development in very acidic rivers. Photo by Jiri Váňa, permission pending.

Figure 35. ***Dicranella heteromalla*** with capsules, a species with attenuated development in very acid water. Photo from Botany Website, UBC, with permission.

Life Strategies and Reproduction

I was surprised at how few studies appeared when I searched Google for aquatic bryophyte reproduction. But at least some studies exist. Field observations have suggested that production of capsules in submersed bryophytes is relatively rare (Carrigan & Gibson 2004; Ares *et al*. 2014). Instead, fragmentation has seemed to be a major strategy.

Like the life forms, the number of life strategies increases as the frequency of submergence decreases for bryophytes associated with Portuguese streams (Vieira *et al*. 2012a, b). Water velocity and hydrologic zone are the primary influences on the life strategies present (During 1979; Lloret 1986; Vieira *et al*. 2012b). The communities that were mostly submersed were characterized by **perennials** and **ephemeral colonists** (Vieira *et al*. 2012b). Those communities that were more frequently emergent had more diversity of life strategies. At higher altitudes, **perennials** seemed to be favored. Hence, **perennials** are more likely in permanent fast-flowing currents, whereas **pioneer colonists** and **colonists** are more common in the lower currents or emergent positions. In those habitats emerged for brief periods each season, **fugitives**, **annual shuttle species**, and **stress-tolerant perennials** were able to colonize deposited sediments.

In their study of environmental drivers for stream bryophytes, Lang and Murphy (2012) concluded that bryophyte abundance in high-latitude streams was typically a function of predominant growth morphology and life strategy. Ock (2014) included life cycle strategies among the adaptations to rheophytic conditions in bryophytes. He described them as mostly **dioicous** (having separate male and female plants) with rare or uncommon sporophytes. This results from the difficulty of travel for the sperm from the **antheridium** (Figure 36) as it attempts to overcome water flow on its way to the **archegonium** (Figure 37-Figure 38) that is located on a different plant.

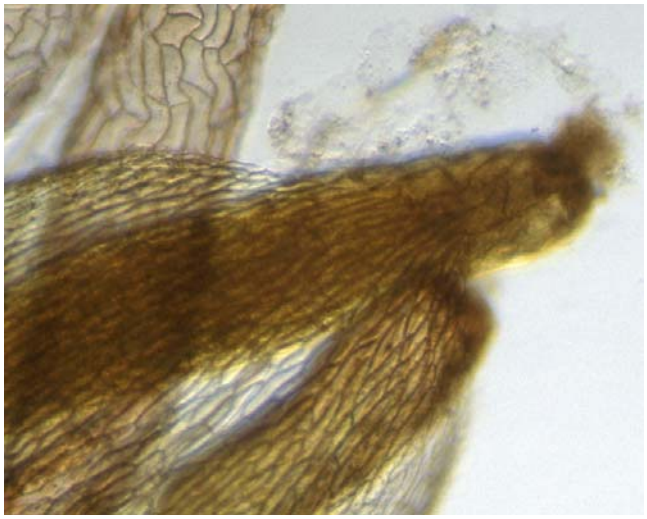

Figure 36. ***Fontinalis duriaei*** antheridia on 13 September 1979 in Coles Creek, Houghton County, Michigan, USA, cultured at 20ºC in artificial stream. Photo by Janice Glime.

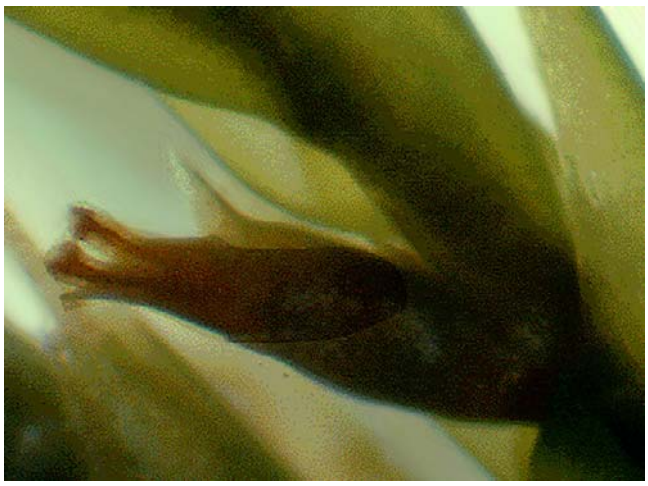

Figure 37. Archegonia of ***Fontinalis*** sp. showing red neck canal cells. Photo by Janice Glime.

Figure 38. ***Fontinalis*** archegonia, with the enlarged one indicating it has been fertilized. Photo by Janice Glime.

Thamnobryum alopecurum (Figure 39) is **dioicous**. During (1978b) found the largest numbers of inflorescences in places with constantly high air humidity. These places also tend to have greater mixing of male and female plants. In drier air, the plants remain mostly sterile. Instead, they develop into large sprouting systems that have little contact between each other. Some even form moss balls in these conditions.

Figure 39. ***Thamnobryum alopecurum*** with capsules, a **dioicous** species with more reproductive inflorescences in places with constantly high humidity. Photo by Snappy Goat, through public domain.

Sexual Strategies and Gametangia

Leitgeb (1868) found antheridia on ***Fontinalis antipyretica*** (Figure 27) from spring until fall, a pattern similar to that which I found in several ***Fontinalis*** species in the Keweenaw Peninsula of Michigan, USA and the long period of development for antheridia is typical of antheridia (see Volume 1, Chapter 5-8). Degree of **apical dominance** (physiological behavior in which the main axis grows more strongly than side branches) is important in determining the location of antheridia and archegonia in ***Fontinalis*** (Berthier 1968). With weak apical dominance, the sexual shoots occur at the axils of the first leaves on side branches. By contrast, when there is strong apical dominance, the main stem forms narrow leaves and these have densely branched first-order sexual shoots in their axils. These first-order shoots occur naturally when the free CO_2 decreases rapidly in the water of late spring, a phenomenon repeated at 8ºC in the laboratory. Apical dominance of the vegetative stem can be increased by cutting off some of the leaves or by using weak illumination.

Carrigan and Gibson (2003) compared the sexuality of species that occurred both streamside and on stream rocks at Cement Creek in the Yarra Ranges National Park, Victoria, Australia. They found that streamside populations had higher numbers of stems, inflorescences, and **gametangia** [archegonia (Figure 37-Figure 38) and antheridia (Figure 36)] than did the same species on stream rocks. The streamside populations of species tested produced more sporophytes than those species on stream rocks. ***Cyathophorum bulbosum*** (Figure 40), however, produced more sporophytes on the stream rocks than did its populations on streamside locations. The gender was generally female-biased for stem numbers and numbers of inflorescences.

Figure 40. ***Cyathophorum bulbosum***, a species that can produce more sporophytes on the stream rocks than do its populations on streamside locations. Photo by John Braggins, with permission.

Berthier (1966) explored the role of light in initiation and development of the sexual organs in ***Fontinalis*** (Figure 27). He found that light influenced both the density and development of buds, with antheridia forming on branches. A low growth rate enabled formation of these antheridial branches. Increased light intensity increased both the density and initiation of these antheridial branch buds.

Fertilization

Goebel (1913, 1915-1918) illustrated development in some of the water mosses, including ***Fissidens*** (Figure 41), ***Fontinalis*** (Figure 27), ***Hygroamblystegium*** (Figure 42), and ***Thamnobryum*** (Figure 39). His drawings included details of archegonia and antheridia. I translated one of his statements to mean that fertilization in ***Fontinalis*** took place in a "glass" of water. A better translation is that the gametangia are suppressed but can be richly formed. The sperm are easily swept away in flowing water. If both archegonia and antheridia are in small water volumes, the ***Fontinalis*** fruits richly. If the sporophytes are not under water, the spores perish. These observations of Goebel emphasize the importance of timing as part of the life strategies. For example, fertilization is likely to be more successful when the water level is low and they can swim without being washed away. In other cases, fast water might be required to splash sperm from males to females. This might mean that only emergent females get fertilized, but at least some should receive sperm.

Figure 41. ***Fissidens fontanus***, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by Matt Keevil, through Creative Commons.

Figure 42. ***Hygroamblystegium fluviatile***, in one of the genera for which fertilization was described by Goebel. Photo by Hermann Schachner, through Creative Commons.

Scapania undulata (Figure 13) is among the widely distributed species of aquatic bryophytes. It grows in shallow streams from boreal regions to subtropical zones (Holá *et al*. 2014). It is dioicous, making fertilization difficult, particularly in its typical submersion in rapid water. But Holá *et al*. (2014) found that it had an "overproduction" of males in 10 streams in southern Finland (100 plots) and suggested that this might be a strategy to overcome sperm dilution in the flowing water, "ensuring" fertilization over longer distances in the water. This male bias contrasts with most dioicous species and seems to relate to its flowing-water habitat. The males and females differ in branching pattern, but no size difference exists. They found few females sex-expressing in the female-only plots and female plants had only one sexual branch per female shoot. The low number of sex-expressing shoots in female-only plots, no co-occurrence of gemmae and female sex organs on a single branch, large number of male plants, and only one sexual branch per female shoot suggest a trade-off between sexual and asexual reproduction and a higher cost for female reproduction.

Belkengren (1962) further learned that sexual reproduction in ***Leptodictyum riparium*** (Figure 43) was induced by a CO_2-free period, followed by addition of CO_2 or sugar. It is a little more difficult to suggest how this might apply in nature, but it could be a change from high temperatures, hence low CO_2, followed by cooler temperatures in which more CO_2 can dissolve in water. Subsequently, it appears that senescence of the plants may induce the formation of sporophytes, perhaps by stopping the production of some inhibitory substance or reduction of photosynthesis.

Figure 43. ***Leptodictyum riparium*** with capsules, a species in which yeast inhibits development from protonemata to the next stage. Photo by Michael Lüth, with permission.

Sporophytes

Aquatic moss sporophytes can be divided into two groups (Vitt 1981). In one group, the gametophytes are aquatic, but the sporophytes are not, often being produced during periods of low water. This includes such taxa as ***Scorpidium*** (Figure 44), ***Hygrohypnum*** (Figure 14), ***Platylomella*** (Figure 45), ***Platyhypnidium riparioides*** (Figure 46), and ***Drepanocladus*** *s.l.* (Figure 3). The other group produces sporophytes that are adapted to the aquatic

habitat. This group of species includes ***Blindia*** (Figure 47), ***Fontinalis*** (Figure 27, Figure 50), ***Scouleria*** (Figure 48), ***Wardia*** (Figure 49), and others with reduced or absence of peristomes, ovate or oblong, smooth, immersed capsules, enlarged perichaetial leaves, and pachydermal exothecial cells.

Figure 44. ***Scorpidium scorpioides*** with capsules, a species that produces these sporophytes while the plant is above water. Photo by Michael Lüth, with permission.

Figure 45. ***Platylomella lescurii***, a species that produces sporophytes while the plant is above water. Photo by Northern Forest Atlas, with permission from Jerry Jenkins.

Figure 46. ***Platyhypnidium riparioides*** with capsules, a species that develops sporophytes above and below water, but the operculum does not dehisce. Photo by J. C. Schou, with permission.

Figure 47. ***Blindia acuta***, a species that produces sporophytes while the plant is below water. Photo by Barry Stewart, with permission.

Figure 48. ***Scouleria aquatica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Matt Goff, with permission.

Figure 49. ***Wardia hygrometrica*** with capsules, a species that typically produces sporophytes while the plant is below water. Photo by Sanbi, with online permission.

Carrigan and Gibson (2004) followed 9 mosses and 7 liverworts, representing 8 and 6 families respectively. They found sexual reproduction, but not in all species. As in the 2003 study, they found that sexual reproduction was lower on stream rocks than in more terrestrial habitats. Asexual reproduction was most important in maintaining colonies compared to sexual reproduction, with all species exhibiting asexual reproduction. There was a female sex bias in all but 2 species. There seemed to be no synchrony of phenological stages.

Landry (1973) collected field-grown capsules of ***Fontinalis dalecarlica*** (Figure 15) in June, 1973, in Plymouth, New Hampshire, USA. These immature capsules were permitted to develop in culture until 27 July 1973, but they remained green and did not appear to be completely mature. Capsules were sterilized, opened, and spores spread on a Chlorophyta medium with 3 ppm tannic acid added. There was still no germination on 10 August when it became necessary to terminate the experiment. This was an unusually late date for capsule maturation compared to what had been observed in prior years, and the sterilization process with 0.1N potassium permanganate may have damaged the spores. The other problem is that the capsules had been transported from New Hampshire to Houghton, Michigan and may have experienced excessive temperatures during the trip.

Kortselius (2003) found that ***Fontinalis antipyretica*** (Figure 27) produces capsules when it is submerged (Figure 50), but he considered dry conditions to be necessary for dehiscence (Figure 51). When desiccation occurs, the operculum is torn loose and lifted off by the hygroscopic movements of the exostome teeth (Figure 52). Spores are released during reversible shape changes in the capsule (Figure 53). It seems that this would require careful timing so that capsules were still pliable when they were desiccated. old capsules have thick walls and are quite hard, seemingly unable to change shape significantly.

Figure 50. ***Fontinalis dalecarlica*** submersed capsules on 26 November 1979 in Fox Run, Plymouth, New Hampshire, USA. Note that the operculum is still intact in the upper mature capsule, but missing in th lower one. Photo by Janice Glime.

Figure 51. ***Fontinalis*** capsule that is shedding its operculum out of water. Photo by Janice Glime.

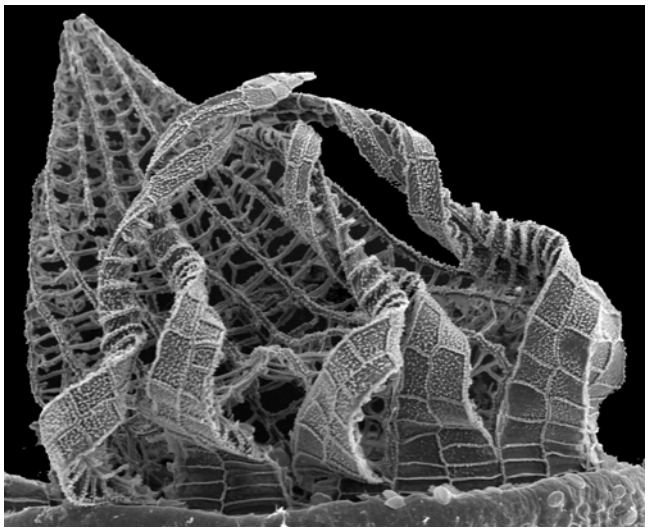

Figure 52. SEM of ***Fontinalis*** peristome showing inner trellis endostome and outer twisted teeth of exostome. Photo by Misha Ignatov, with permission.

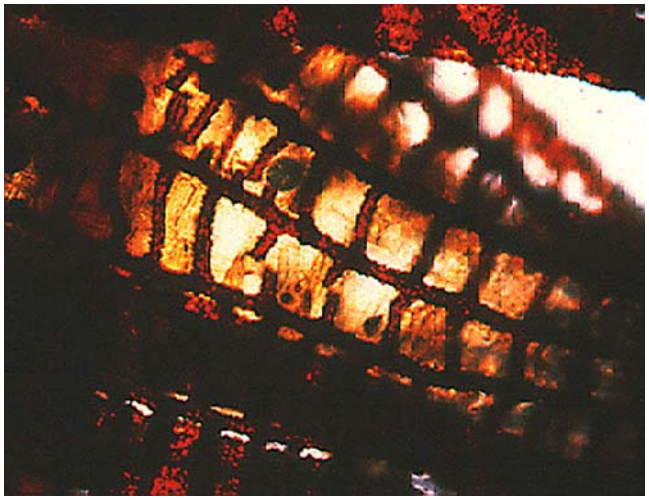

Figure 53. Trellis peristome of ***Fontinalis*** showing green spores among the teeth. Photo by Janice Glime.

During (1978a) found capsules on ***Fontinalis antipyretica*** (Figure 27) 30 April-2 May, but his short note did not indicate the degree of maturity. In my own studies I did not find this species with capsules, but this species was not nearly as common as other ***Fontinalis*** species in the areas that I studied.

Although ***Fissidens fontanus*** (Figure 41) produces capsules in the USA and Europe, capsules were unknown in Mexico. Pursell (1992) reported these in Mexico for the first time. However, no data were available on timing of capsule production. The capsules were illustrated, demonstrating the short seta compared to some species of ***Fissidens***. The capsule likewise was quite small, with an urn only about 0.2-0.3 mm long in the one illustrated.

Lawton (1966) reported capsule production in ***Hygrohypnum bestii*** (Figure 54). This was the first time that the sex organs and capsule had been described in this dioicous species. The species occurs in montane streams, typically at 1500-3000 m elevation, on wet rocks that are often covered with silt.

Figure 54. ***Hygrohypnum bestii***, a **dioicous** species that rarely produces capsules. Photo by Robin Bovey, with permission through Dale Vitt.

One of the reasons for the lack of capsule observations may be the timing of their presence (Glime 2014). In a stream in New Hampshire, USA, both ***Fontinalis dalecarlica*** (Figure 15) and ***F. novae-angliae*** (Figure 23) produce their capsules in the freezing waters of winter. The capsules are badly eroded by the spring runoff, and it seems likely that this is a major vehicle for spore dispersal. By the time the snow is gone, most of the capsules have disappeared, and only a few damaged capsules remain. Their appearance at that time suggests that it is abrasion, not loss of operculum, that permits spore dispersal.

The timing in Finland does not seem to fit this pattern. Kotilainen (1927) found capsules on ***Fontinalis dalecarlica*** (Figure 15) on 6 July 1925 in Finland.

Dispersal

Few studies have addressed dispersal in aquatic bryophytes. Miller (1985) examined subfossils of a number of bryophyte fragments in late Pleistocene deposits buried in sediments in the northeastern United States. These suggested that the fragments had served as propagules dispersed by wind and melting glaciers. Many of the fragments had shoots extending from them, supporting the notion that these were serving as propagules.

Elssmann (1923-1925) commented on the fact that capsules of ***Fontinalis antipyretica*** (Figure 27) retained their lids (Figure 51). He noted that Grimme had mentioned that the shedding of the operculum may be delayed until April of the next year, attributing this to the fact that the plants remain submersed. Rather, at least in culture, the capsules themselves were eventually shed several months after maturity, falling to the bottom of the culture dish. There they gradually died, as did the spores inside. Grimme had reported capsule ripening in August, so Elssmann harvested capsules from his cultures at the beginning of July and found them to contain spores with abundant chlorophyll. When the spores were then cultured, nearly all had germinated within 18 days. Elssmann also cultured capsules on moist sand starting in April. These drier capsules likewise failed to lose the operculum. But the spores developed as they had in the submersed capsules. The same behavior occurred in ***Cinclidotus fontanus*** (***C. fontinaloides***?; Figure 55), ***Fissidens fontanus*** (Figure 41), and ***Platyhypnidium riparioides*** (Figure 46). This begs the question, then, how do the spores escape the capsule? The image in suggests that they do indeed dehisce in nature.

Figure 55. ***Cinclidotus fontinaloides*** with capsules that have lost their opercula. Photo by Hermann Schachner, through Creative Commons.

Hydrochory

Hutsemekers *et al*. (2013) addressed the question of dispersal somewhat indirectly by examining gene flow in ***Platyhypnidium riparioides*** (Figure 46). They summarized the assumed effects of **hydrochory** (dispersal by water): decreases or erases patterns of isolation by distance, increases outbreeding, and results in downstream increase in genetic diversity. They found that the geographical partitioning of genetic variation was "substantial" in the river basin. Using this as indirect measurement of dispersal, they found that the overall dispersal ability of moss diaspores, including fragments, was weaker than that of pollen or windborne seeds. Thus, these spore-producing plants suffer from the severe limitations of clonal dispersal and establishment. Hydrochory does not enhance dispersal and fertilization, at least in ***P. riparioides***. Instead, the genetic structure suggests clonality and discrete events of spore migration, with the **unidirectional diversity/dispersal hypothesis** (downstream hydrochoric spread of propagules of aquatic and riparian plant species, without upstream compensation, can be expected to result in downstream accumulation of population genetic diversity) being unsupported by this species. Rather, **metapopulation** (group of populations separated by space but are same species) processes apply to this aquatic moss. As the concept of metapopulation implies, such spatially separated populations interact as individual members move from one population to another. This can occur through spores, fragments, or specialized vegetative propagules.

Certainly ***Fontinalis*** species benefit from downstream dispersal in flow. This is possible because vegetative propagation is usually successful in these species (Welch 1948). In fact, biologists with the Burley Irrigation District in Cassin County, Idaho, USA, complained that it (***Fontinalis duriaei*** – Figure 56-Figure 57) "catches on almost anything and holds silt, forming mounds in the canals. It is hard to kill, and costs considerable to keep it out." When wounded, stems of ***Fontinalis*** will produce protonemata at the site of a broken stem (Figure 58). Removal of the stem tip can result in new branches below the apex in several ***Fontinalis*** species (Figure 59-Figure 61).

Figure 57. Detached ***Fontinalis duriaei*** caught on wood in Gardner's Creek, Michigan, USA. Photo by Janice Glime.

Figure 58. Protonemata growing from broken tip of ***Fontinalis hypnoides***. Photo by Janice Glime.

Figure 56. ***Fontinalis duriaei***, a species that is rejected by Rainbow Trout, but that passes through the digestive tract mostly without physical damage. Photo by Michael Lüth, with permission.

Figure 59. ***Fontinalis antipyretica*** wound rhizoids and a new branch just below the broken tip. Photo by Janice Glime.

Figure 60. ***Fontinalis squamosa*** branch below broken tip, exhibiting phototropism to a light source at the left. Photo by Janice Glime.

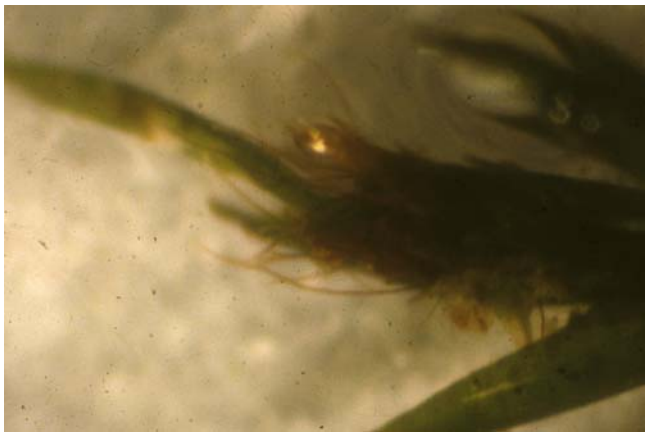

Figure 61. ***Fontinalis squamosa*** with broken tip and a new branch initiating just below that break. Photo by Janice Glime.

Welch (1948) noted that ***Fontinalis sphagnifolia*** (Figure 62) produces "rhizomes" with numerous rhizoids. This permits it to spread, but also provides a base ready for establishment in a new site when it gets carried downstream by water flow. The effectiveness of flow dispersal is suggested by observations of ***Fontinalis*** in a series of connected moraine ponds (Sayre 1945).

Figure 62. ***Fontinalis sphagnifolia***, a species that produces rhizomes with numerous rhizoids. Photo by Will Van Hemessen, through Creative Commons.

Korpelainen *et al*. (2013) used genetic markers in three clonal aquatic moss species in a connected lake system. They found a mean genetic diversity per population of 0.138 for ***Calliergon megalophyllum*** (a quiet water species; Figure 63), of 0.247 for ***Fontinalis antipyretica*** (slow to moderately rapid water; Figure 27, Figure 30), and of 0.271 for ***Fontinalis hypnoides*** (moderately rapid water; Figure 64). The total diversity of their populations in the connected lake system was 0.223, 0.385, and 0.421, respectively. Although the differences were significant, there was evidence of a moderate amount of gene flow within this system. The researchers suggested that both water flow and animal vectors, including water flow, dispersed these three bryophytes. Furthermore, the genetic structure suggests that fragments are the major contributors to this dispersal.

Figure 63. ***Calliergon megalophyllum***, a species that might be dispersed by both water flow and animal vectors. Photo from Earth.com, with permission.

Figure 64. ***Fontinalis hypnoides***, a species that can regenerate from broken stem tips. Photo by Ivanov, with permission.

Dispersal Vectors

One of the problems of dispersal in aquatic habitats is isolation (Figuerola & Green 2002). While streams can carry propagules downstream, they cannot carry them to a different stream or disconnected lake. Many rarely produce

spores that could be transported by wind to a different water body. But recent studies have indicated that waterbirds can facilitate dispersal. Fortunately, even small fragments of leaves can develop new plants, and these can easily be transported by feathers and feet. And some may survive gut transport.

Lazarenko (1958) considered long-distance dispersal of moss spores unlikely, considering their dispersal to follow patterns like those of tracheophytes. Rather, he considered there to be polytopic origins to account for disjunctive species. While the dispersal of spores in ***Fontinalis*** (Figure 56-Figure 62) seems to be facilitated by abrasion and flowing water (Glime *et al*. 1979), the lack of dehiscence in most capsules would seem to support Lazarenko's suggestion. On the other hand, fragments can travel relatively long distances in the flow, and water birds might carry the moss fragments in their feathers. It is likely that bears and other mammals can carry the fragments in their fur and claws.

Proctor (1961) demonstrated that the liverwort ***Riella*** (Figure 65-Figure 66) spores can be dispersed by waterfowl. Mallard ducks were placed in a pen with ***Riella*** having mature spores. The ducks consumed the liverworts immediately. Feces were collected 50 minutes later and examined. Many individual spores were present, but there were no intact sporophytes and all the fragments were dead. Spores subsequently stored in water at 24ºC germinated after 60 days.

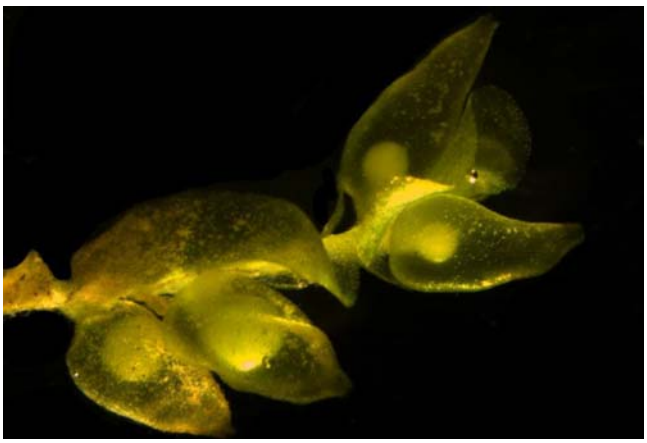

Figure 65. ***Riella helicophylla*** showing capsules. Photo by NACICCA through Creative Commons.

Figure 66. ***Riella cossoniana*** showing spores that can be dispersed by ducks. Photo by Jan-Peter Frahm, with permission.

Laaka-Lindberg *et al*. (2003) reviewed dispersal of asexual propagules in bryophytes. They also noted that migrating birds, especially waterfowl, can carry vegetative attached to the mud on their feet (see also Davison 1976). Such a possibility for the floating liverworts ***Ricciocarpos natans*** (Figure 67) and ***Riccia fluitans*** (Figure 68) was suggested by Buch (1954). It would be interesting to see if these two species are eaten by waterfowl, especially as they accompany duckweed, and if they can germinate from the feces. Frahm (2007) also assumed that the worldwide distribution of ***Ricciocarpos natans*** had been facilitated by waterfowl.

Figure 67. ***Ricciocarpos natans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Janice Glime.

Figure 68. ***Riccia fluitans***, a floating liverwort with the potential of dispersal by waterfowl. Photo by Štěpán Koval, with permission.

Lewis *et al*. (2014) brought further credence to these suggestions by showing correlations between transhemispherical migratory routes of shorebirds and the bipolar disjunctions in bryophytes. They then examined a

number of birds in their Arctic breeding grounds, finding bryophyte propagules, among other propagules, clinging to the feathers. Eight species of these migrant waders had bryophyte diaspores among their feathers. The propagules were so common among the feathers that they suggested the entire population could potentially carry viable plant parts during migration.

It is possible that fish aid in the dispersal of aquatic mosses. Since the mosses provide cover for a number of aquatic insect species (Glime 1994; see Volume 2), they are a good site for foraging by fish. It is likely that at least occasionally the fish may ingest bits of mosses. Paulson (1980) collected a "packet" of feces (Figure 69) from Rainbow Trout (*Oncorhynchus mykiss*) that was comprised mostly of ***Fontinalis duriaei*** (Figure 56). The moss was bright green when it was expelled. It was placed in a baby food jar in the artificial stream, but by the second day it had lost its green color. If it had been deposited in a stream instead of such a confined space, the associated gut contents would have been diluted and might not have the same effect on the moss, perhaps permitting its survival. If so, this would be a potential mechanism for moving the mosses upstream as well as downstream for dispersal. However, I must point out that the moss had to be force-fed to the fish, so I suspect this mode of dispersal is rare.

Figure 69. ***Fontinalis duriaei*** in feces from force-fed Rainbow Trout. Photo by Janice Glime.

Boch *et al*. (2013) reasoned that slugs might be good dispersal agents for bryophyte spores since they often eat spores (Figure 70). But could the spores survive the digestive tract? They fed capsules of several bryophyte species to three species of slugs. They found an overall germination rate of 51.3% of bryophyte spores from the 117 samples. Among these was the streambank species ***Apopellia endiviifolia*** (Figure 71). There was little difference evident among the bryophyte species, but there was strong variation among the spores from the three slug species (Figure 72): ***Arion vulgaris*** (Figure 73), ***Arion rufus*** (Figure 74), ***Limax cinereoniger*** (Figure 75).

Figure 70. ***Ariolimax*** *cf*. ***californicus*** feeding on ***Asterella*** archegonial head and possibly the spores. Photo by Tom Voltz, with permission.

Figure 71. ***Apopellia endiviifolia*** with capsules. The spores can survive slug guts, a possible dispersal means. Photo by Janice Glime.

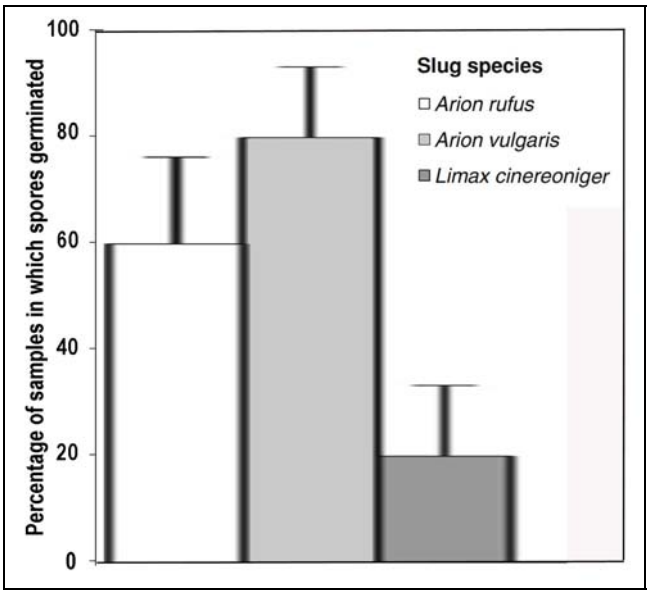

Figure 72. Slug gut dispersal of ***Apopellia endiviifolia*** spores. Modified from Boch *et al*. 2013.

Figure 73. ***Arion vulgaris*** on bryophytes, a slug that can potentially disperse spores of streamside bryophytes. Photo by F. Welter-Schultes, animalbase.uni-goettingen.de, through public domain.

Figure 74. ***Arion rufus*** on ***Sphagnum***, a potential endochorous bryophyte spore disperser. Photo by Walter Siegmund, through Creative Commons.

Figure 75. ***Limax cinereoniger*** feeding on lichen, a potential endochorous bryophyte spore disperser. Photo by H. Krisp, through Creative Commons.

Not only do bryophyte fragments get dispersed by wind and water, but so do their inhabitants. Bitušík *et al*. (2017) demonstrated that larvae of the chironomid (midge) ***Micropsectra uliginosa*** (Figure 76) travel in fragments of aquatic mosses, including ***Hygrohypnum*** sp. (*e.g.* Figure 14, Figure 54). This facilitates short-distance dispersal of the species, including the flightless males, albeit in their larval stage. They found detached moss tufts with chironomid larvae in their pan traps and assumed that these mosses had been flushed first by water, then trapped behind rocks or other obstructions in shallow water. Subsequently strong winds and gusts could lift the mosses and their inhabitants to mossy habitats above water nearby.

Figure 76. ***Micropsectra*** sp. larva; ***Microspectra uliginosa*** can be dispersed by blowing moss fragments. Photo by Aina Maerk Aspaas, NTNU University Museum, through Creative Commons.

Changes in Distribution

Frahm and Abts (1993) demonstrated the rapidity of dispersal of a number of aquatic species in the lower Rhine, Germany. From 1972 until 1992, the initial eight species were joined by ten more. The greater number of species in 1992 was attributed to improvement in water quality.

Frahm (1997) documented the distributional increase of aquatic mosses in the Rhein, Germany. ***Cinclidotus danubicus*** (Figure 77) has spread from its 1911 location to the Upper Rhine and Netherlands in 1997. ***Cinclidotus riparius*** (Figure 78) has spread northward. ***Fissidens arnoldii*** (Figure 79) spread from the Upper Rhine to the Lower Rhine in 70 years. ***Fissidens fontanus*** (Figure 41) was first recorded in the Upper Rhine in 1968 and by 1997 it had spread extensively along rivers in Central Europe. ***Hyophila involuta*** (Figure 80) spread 100 km northward along the Upper Rhine from 1927 to 1964. ***Fissidens rivularis*** (Figure 81) and ***Orthotrichum sprucei*** (Figure 82), both previously known only from British Isles, Belgium, and The Netherlands, have spread to the Rhine and its tributaries.

Figure 77. ***Cinclidotus danubicus***, a species that has spread in the Rhein (Rhine) since 1911. Photo by Michael Lüth, with permission.

Figure 78. ***Cinclidotus riparius***, a species that has spread northward in Germany. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Fissidens arnoldii***, a species that spread from the upper to the lower Rhein (Rhine) within 70 years. Photo by Michael Lüth, with permission.

Figure 80. ***Hyophila involuta***, a species that has spread rapidly among rivers in Central Europe. Photo by Bob Klips, with permission.

Figure 81. ***Fissidens rivularis***, a species that has spread rapidly and recently in Europe. Photo by David T. Holyoak, with permission.

Figure 82. ***Orthotrichum sprucei***, a species that has spread rapidly and recently in Europe. Photo by Michael Lüth, with permission.

Small Dispersal Units and Long-distance Dispersal

Heino *et al*. (2012) concluded that organisms with small propagules such as ferns and bryophytes may have weak geographical variation over broad areas due to unlimited dispersal. They found that environmental factors were most important in boreal headwater streams. The

bryophyte data seemed to be better explained by environmental variables than by spatial characters.

Finlay (2002) contended that organisms less than 1 mm in size generally occur worldwide (the "everything is everywhere" hypothesis; see Vol. 1, Chapt. 4-8), whereas larger organisms are more restricted. He supported this with data on 1278 species of freshwater pond eukaryotic organisms showing that they were cosmopolitan. It follows that if the propagules are less than 1 mm, like bryophyte spores, they should follow the same principle. Kyrkjeeide *et al*. (2014) demonstrated a negative correlation of range with spore size of bryophytes in Europe based on spores up to 40 µm in diameter. In this case, those bryophytes reproducing (producing spores) less frequently had greater genetic differentiation than did bryophytes with frequent reproduction (p=0.04). Van Zanten (1978a, b) supported the possibility of long-distance travel of at least some species by placing the spores on airplane wings for trans-oceanic travel. Among these were the aquatic ***Warnstorfia fluitans*** (Figure 83) and ***Leptodictyum riparium*** (Figure 43), which could survive desiccation up to 13 months.

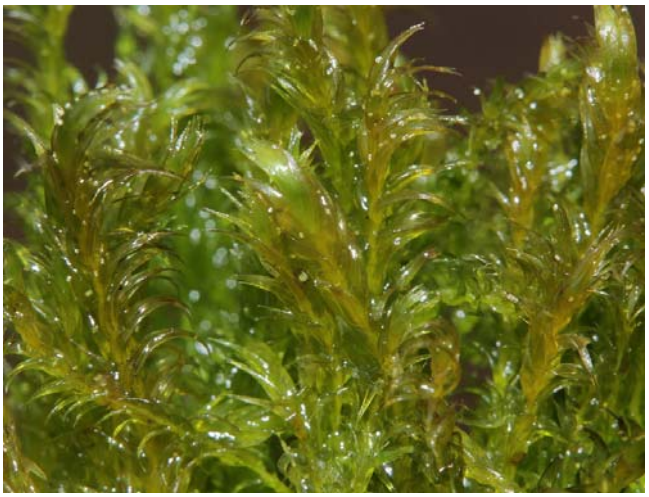

Figure 83. ***Warnstorfia fluitans***, a species in which spores can survive conditions necessary for long distance travel. Photo by Hermann Schachner, with permission.

Santos *et al*. (1996) collected airborne spores and other propagules on agar in Petri dishes. Once germinated, the collections revealed the presence of the bryophytes ***Fossombronia angulosa*** (Figure 84), ***Pellia epiphylla*** (Figure 6), ***Leptodictyum riparium*** (Figure 43), ***Bryum dunense*** (Figure 85), ***Ditrichum*** sp. (Figure 86), ***Gymnostomum calcareum*** (Figure 87), ***Pottia*** sp. (probably now in ***Tortula***; Figure 18), and ***Trichostomum brachydontium*** (Figure 88). Of these, ***Pellia epiphylla*** is a common streambank species and ***Leptodictyum riparium*** lives submersed in quiet water. It is also notable that a number of **Cyanobacteria** (Figure 89) arrived, providing potential nitrogen-fixers to associate with the bryophytes. Of the taxa collected, 75% were spores <25 µm. These successful spores suggest that diaspore banks can be important sources to recolonize a stream when it is disturbed or changes channel location.

Figure 84. ***Fossombronia angulosa***, a species that grew from collected spores. Photo by Jan-Peter Frahm, with permission.

Figure 85. ***Bryum dunense***, a species that grew from collected spores. Photo by Michael Lüth, with permission.

Figure 86. ***Ditrichum gracile***; ***Ditrichum*** sp. grew from collected spores. Photo from Snappy Goat, through public domain.

Figure 87. ***Gymnostomum calcareum***, a species that grew from collected airborne spores. Photo by Larry Jensen, with permission.

Figure 88. ***Trichostomum brachydontium***, a species that grew from collected airborne spores. Photo by David T. Holyoak, with permission.

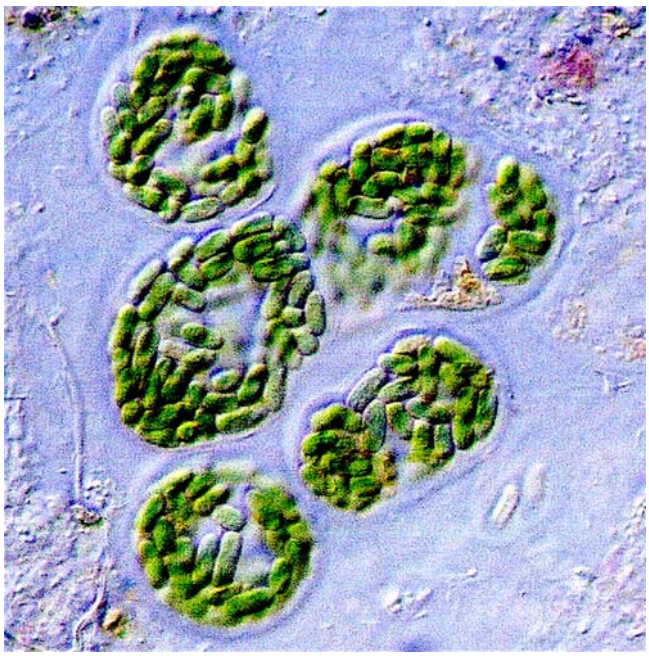

Figure 89. Cyanobacterial mat. **Cyanobacteria** germinated from airborne collections. Photo from NASA, through public domain.

Spore Germination and Protonema Development

Spore germination and protonema development have been studied in a number of bryophytes, including aquatic species (Kanda & Nehira 1976). These are illustrated and early stages following germination are described for the aquatic mosses ***Leptodictyum riparium*** (Figure 43) and ***Cratoneuron filicinum*** (Figure 90).

Figure 90. ***Cratoneuron filicinum***, one of the aquatic species for which protonema development was described by Kanda and Nehira (1976). Photo by J. C. Schou, with permission.

Glime and Knoop (1986; Glime 2014) concluded that ***Fontinalis squamosa*** (Figure 91) is an opportunist that releases spores (Figure 92) from multiple capsules over a relatively long period. This extended period of spore release may be the result of having fertilization over an extended time. Glime (1984) demonstrated that ***F. dalecarlica*** (Figure 15) produces mature archegonia over several months. A single collection of ***F. squamosa*** likewise provided both antheridia (Figure 36) and archegonia (Figure 37-Figure 38) in various stages of development. Capsules were also present in this single collection and similarly were in various stages of development. This spread of maturation could provide spores at different conditions of flow, and increase opportunities for at least some spores to meet favorable conditions. Elssmann (1923-1925) found that spores in capsules exposed to air ripened several weeks earlier than those that were submersed, providing further variability in response to changing water levels.

Figure 91. ***Fontinalis squamosa***, a species that produces both chloronemata and caulonemata. Photo from <www.aphotofauna.com>, with permission.

Figure 92. Longitudinal section of ***Fontinalis squamosa*** capsule showing green spores. Photo by Janice Glime.

Fontinalis squamosa (Figure 91) exhibits another potentially adaptive trait. Its spores within a single capsule (Figure 92) do not all mature at the same time. As the spores develop, some abort (Figure 93) (Glime 1983; Glime & Knoop 1986; Glime 2014). Others enlarge and are bright green, while some remain smaller and may be only partially green. Both can germinate, but the larger ones germinate more quickly (5 days) and have a higher germination success than the small ones (18 days). The protonemata in this species are also negatively **phototropic** (Figure 94) (Glime 2014). This habit of growing away from the light source may be adaptive in keeping them under water. It would be interesting to see if there is a threshold light level that elicits this phototropic response.

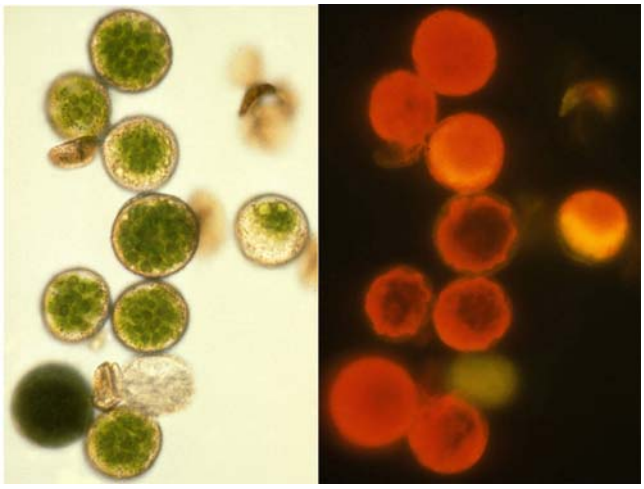

Figure 93. ***Fontinalis squamosa*** spores; those with clear areas on the left and yellow areas on the right are abortive. Those on the right are indicating chlorophyll fluorescence, showing red. Photos by Janice Glime.

Figure 94. ***Fontinalis squamosa*** protonemata singles typical of those grown at 3ºC. Light is coming from the lower right corner, indicating these protonemata are negatively phototropic. Photo by Janice Glime.

Glime and Knoop (1986) described the spore germination and development of ***Fontinalis squamosa*** (Figure 91). This moss develops both **chloronemata** (Figure 95) (protonemal filaments with many well developed chloroplasts and perpendicular cross walls) and **caulonemata** (protonemal filaments with fewer, less well developed chloroplasts and oblique crosswalls; portion of protonema that generates buds when both protonemal types are present). They can grow straight with no branches or have multiple branches, depending on lighting conditions. But buds failed to develop in the laboratory cultures until some of the abandoned plates became contaminated with fungi, suggesting that some developmental hormone might be supplied by the fungi.

Figure 95. ***Fontinalis squamosa*** branched protonema, with **caulonemata** forming at the tips of the branches, exhibiting lighter coloring due to fewer chloroplasts. This growth form was typical of cultures at 20ºC. Photo by Janice Glime.

Physiological conditions and environmental signals that are important to the developmental stages of aquatic bryophytes are poorly known. Belkengren (1962) experimented with ***Leptodictyum riparium*** (Figure 43) under a variety of conditions. Yeast inhibits its shoot growth in culture. But protonemal growth is not affected. Yeast causes death to shoot buds. As a result, the moss grows in the presence of yeast and never reaches another stage. Could this be the sort of interaction that maintains ***Dicranella heteromalla*** (Figure 35) in a protonema stage in

the water (Higuchi *et al*. 2003)? The acid environment would be favorable to growth of fungi. Or is it some nutrient level?

Temperature can play a role in both germination success and form of the protonemata (Glime & Knoop 1986). At 3ºC, no spores germinated in culture, although distention occurred. At 20ºC, the protonemata grew aerially away from the agar and toward the light source, subsequently forming balls of irregular filaments with rounded cells.. The best growth was exhibited by cultures at 14ºC, with greater growth on the unshaded side of the plate. Growth forms differed with temperature (Figure 94-Figure 96). Nishida and Iwatsuki (1982) considered the protonema type to be adaptive, reflecting habitat more than its taxonomic affinity. Bud development did not occur until 3 months after the cultures were started, and the presence of buds was restricted to contaminated cultures, suggesting that the fungus might provide a needed stimulant to the bud development (Glime & Knoop 1986). Rhizoids formed before leaves at about an 8-cell stage.

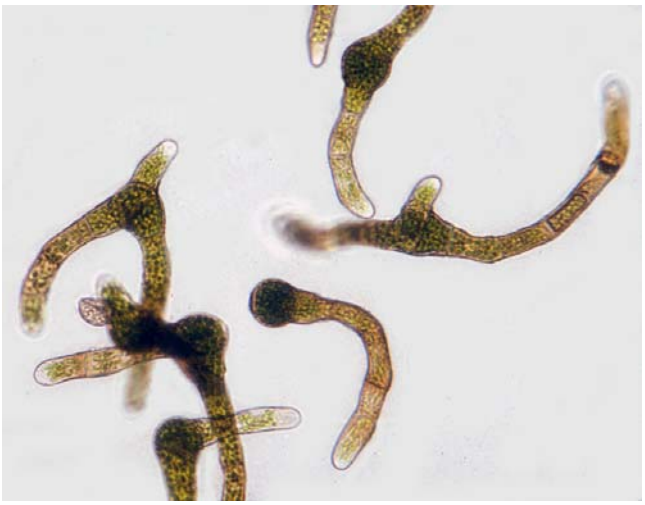

Figure 96. ***Fontinalis squamosa*** protonemata with mostly 2 branches from the spore, typical of protonemata grown at 14ºC. Photo by Janice Glime.

Asexual Reproduction

Carrigan and Gibson (2003) concluded that reproduction of stream bryophytes is primarily asexual. This is supported by evidence that most fragments of these bryophytes seem able to develop new plants in nature. For example, Glime (1970) found a fragment of ***Scapania undulata*** (Figure 13, Figure 97) leaf with a new plant growing from the center of the leaf, even though this species is also able to produce gemmae. I don't know if it was able to develop rhizoids to attach, but as the new shoot got larger, I would expect it to be able to develop rhizoids at the leaf nodes.

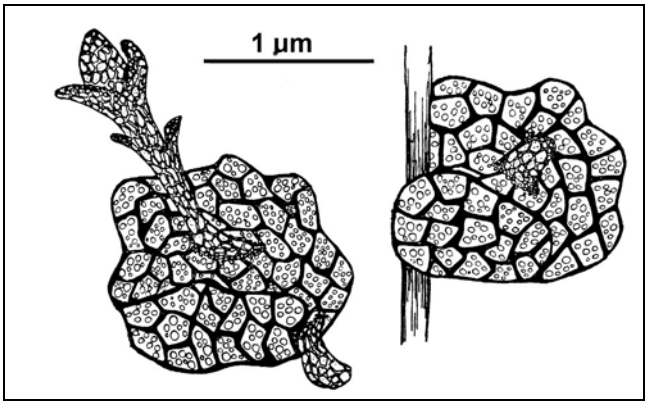

Figure 97. ***Scapania undulata*** plantlets from detached leaves of ***S. undulata*** in March 1969 in a stream near Plymouth, NH, USA. Drawings by Flora Mace.

It is likely that aquatic species are more successful at making new colonies from fragments because of their aquatic habitat. If a fragment arrives in a new location, it most likely arrived with flowing water and lodged somewhere that was wet. This would permit it to develop a new plant while it remains wet, whereas in the terrestrial environment new arrivals have a much greater chance of drying out and losing vigor before a new plant can begin growth or become established.

Regeneration

With the difficulty of accomplishing sexual reproduction and spore dispersal, fragmentation becomes more important. For this to succeed, these fragments must be able to dedifferentiate and regenerate new branches and whole colonies.

Regeneration is common among bryophytes. Giles 1971) describes the dedifferentiation and regeneration. Kreh (1909 in Giles 1971) demonstrated that every part of a liverwort except the antheridia could be induced to regenerate. Even diploid gametophytes can develop from pieces of a seta. In ***Plagiomnium affine*** (Figure 98), if a leaf remains on the stem it does not dedifferentiate. However, if it is removed from the stem in appropriate light, the leaf will dedifferentiate and redifferentiate to form **secondary protonemata**.

Figure 98. ***Plagiomnium affine***, a species that can regenerate from a detached leaf. Photo by Hermann Schachner, through Creative Commons.

Gimeno and Puche (1998) followed the responses of ***Platyhypnidium riparioides*** (Figure 99) in a polluted stream to assess damage to the moss and regeneration. They found that it produces caulonemata at the leaf bases of apical branches. Buds form while these filaments are still attached. When these sets of leaves become detached following **necrosis** (cell death), they can disperse. Rhizoids eventually develop, permitting these fragments to attach in a new location. In the lab, newly cut fragments developed the caulonema in only 5 days and buds arose in 11 days. Rhizoids developed in 21 days. Fragments and damaged leaves were common in the stream and the researchers suggested that in the apparent absence of sporophytes this was the major means of reproduction.

Figure 99. ***Platyhypnidium riparioides***, a species that can form new buds and rhizoids on detached pieces. Photo by Hermann Schachner, through Creative Commons.

Heald (1898) was unsuccessful in his attempts to regenerate ***Fontinalis antipyretica*** (Figure 27). He cultured leaves and stems in water, on earth, and with varying amounts of moisture with no success. On the other hand, I have successfully cultured broken stems of ***Fontinalis squamosa*** (Figure 60), ***F. hypnoides*** (Figure 64), and observed protonemata growing at the broken tips (Figure 58) of the latter. ***Fontinalis dalecarlica*** instead produced rhizoids from detached terminal buds (Figure 100) and leaves (Figure 101). I was also able to grow 2-cm pieces of ***F. antipyretica*** in artificial streams.

Figure 100. Unattached tip of ***Fontinalis dalecarlica*** developing rhizoids, hence serving as a propagule. Photo by Janice Glime.

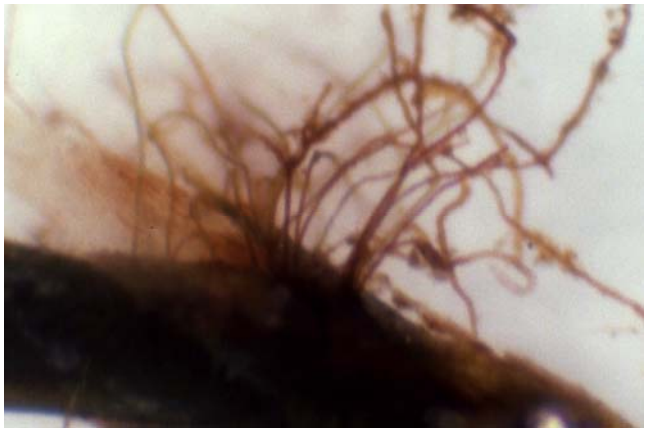

Figure 101. Rhizoids on detached leaf of ***Fontinalis dalecarlica***. Photo by Janice Glime.

The aquatic moss ***Fontinalis antipyretica*** (Figure 27) is capable of regeneration from nearly every part of the gametophyte (Ares *et al*. 2014). She was able to regenerate plants from cortical cells in the bases of detached shoots, margins and abaxial surfaces of leaves, stems with leaves removed, and laminae of detached leaves. These plant parts produce a variety of filament systems, including protonemata with short rectangular cells with transverse crosswalls, and unbranched rhizoids.

Fissidens fontanus (Figure 41) can regenerate even from its calyptra (Figure 102, Britton 1902). The capsules fall from the plants before they mature and the calyptra is still retained. Both the capsule and calyptra can float, so both can act as dispersal units. Goebel (1915-1918) also reported such a capsule of ***Fissidens fontanus*** with a young shoot emerging from beneath the calyptra (Figure 102); it even is producing an archegonium.

Figure 102. ***Fissidens fontanus*** calyptra exhibiting germination of a new shoot. Photo courtesy of Hans Kruijer.

Gemmae and Bulbils

Little has been written about gemmae and bulbils in truly aquatic bryophytes, especially in mosses. One study

of interest is the induction of vegetative propagules in ***Porella pinnata*** (Figure 103). The leafy liverwort ***Porella pinnata*** did not fare well when cultured in moist chambers, with fungi and algae developing (Fulford 1944). However, when two cultures were transferred to nutrient media and given regular nutrient treatments and dim light, they developed vegetative propagules, ranging from bulging leaf cells to leafy shoots.

Figure 103. ***Porella pinnata***, a floodplain species that develops growths of fungi and algae when cultured in moist chambers. Photo by Alan Cressler, with permission.

Ares *et al*. (2014) discovered that the aquatic moss ***Fontinalis antipyretica*** produces gemmae. Filamentous gemmae are freed by **schizolysis** (splitting and breaking apart). Spherical brood cells are produced in ageing and desiccating cultures. Ares and coworkers suggested that these asexual propagules may occur in response to falling water levels in nature. These previously unknown means of reproduction may be important in spread and spatial genetic structure. These researchers also suggested that differences between axenic and contaminated cultures may be due to positive associations between the moss and bacterial or fungal contaminants.

Could there be other protonematal gemmae from other aquatic species hiding in the ecosystem, undiscovered because the protonemata are so difficult to find in nature?

Longevity

For many bryophytes that are not securely attached to the substrate, the living portion may only reflect a few years, whereas older basal portions are senescing or dying at the same rate. However, for a stream bryophyte, attachment makes decomposition of the basal portions a bigger problem. It is not unusual, however, to find basal portions that have lost their leaves, but the apical portions are vibrant, living plants. Therefore, **longevity** of the whole plant is an important part of a successful strategy, especially for **streamer** life forms.

Estimating the age of aquatic bryophytes can be challenging. Frye (1928) estimated the ages of a number of bryophytes based on apical regions that survived the winters, but none of these was submersed. These terrestrial bryophytes, including several streambank species, ranged up to 6 years of age present. I would estimate that ***Fontinalis*** (Figure 27) lives considerably longer than that, although the basal portions may be devoid of leaves. I grew a number of species in the lab and found that they could rebranch 1-2 times in just 15 weeks, so it does not appear that counting branches would be a useful indicator.

Life Cycle Strategy

All of these life cycle strategies work together to make a successful life cycle (Figure 104). Spore germination in the field is unknown for most aquatic species, but for ***Fontinalis novae-angliae*** and ***F. dalecarlica*** the capsules are produced in the winter and can release spores during early spring runoff. At the same time, the plants experience scouring and dispersal of fragments. In the later spring, when there is good sunlight and the trees do not yet form a canopy, growth and branching are at their best. In the summer, when temperatures rise and water levels drop, the rhizoids have their greatest growth. By fall, water levels rise again, temperatures cool, and days are shorter. Archegonia mature, reaching maturity as the longer-developing antheridia also mature. If the water level permits some branches to be wet, but above water, sperm can be splashed to new plants and accomplish fertilization.

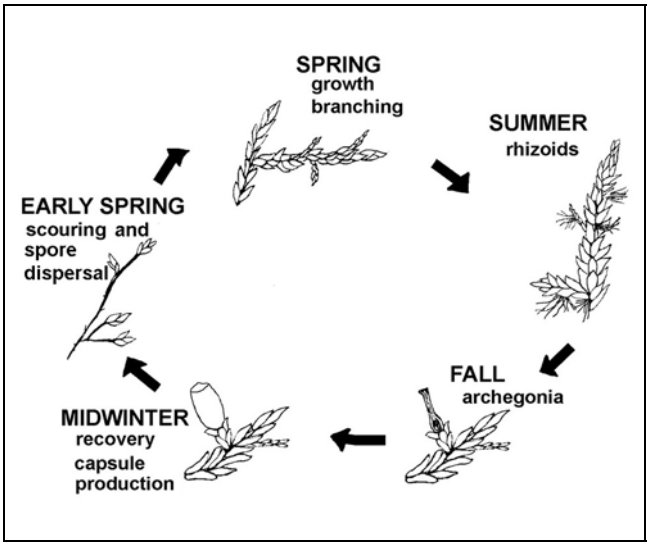

Figure 104. ***Fontinalis novae-angliae*** (Figure 23) and ***F. dalecarlica*** (Figure 15) seasonal life cycle. Diagram by Janice Glime.

Heino and Virtanen (2006) provide a good summary of the interrelationship of life strategies and stream bryophyte success. They considered that bryophytes could be divided into dominants and transients/subordinates. These two groups had sharp differences in life-history strategies and growth/life forms. They concluded that the abundance-occupancy relationships suggest that dispersal limitation and metapopulation processes may be the governing factors for the dynamics of the aquatic bryophytes, whereas in the semi-aquatic habitat, habitat availability may be more important in contributing to regional species occupancy.

The next subchapter will further discuss the physiological factors relating to the reproductive cycle. These will include temperature and light effects on the induction of reproductive structures.

Summary

Life forms are environmental expressions, whereas **growth forms** are genetically controlled. Both help to determine the suitability of the species for survival in streams. In fast water, these life forms include **streamers**, especially in permanently submersed sites. Other dominant forms include **smooth mats**, **tall turfs**, **fans,** and **short turfs**. Plasticity of life forms permits a species to occupy a wider range of moisture habitats, with stem elongation typically occurring in submersed conditions.

Asexual reproduction predominates; fertilization is difficult under water, particularly for dioicous species. Sporophytes are often emergent, even if the leafy portion is under water. For those submersed capsules, there is evidence that dehiscence might only occur when the capsule becomes emergent, or not at all. Fragments are particularly common as propagules. These can be dispersed by flowing water and animals, and once on land some might be dispersed by wind. Waterfowl might be especially important vectors for long-distance dispersal. The life cycle strategy seems to optimize energy and take advantages of the changing conditions with seasons. For example, in several ***Fontinalis*** species, spring is important for growth, summer for rhizoids, fall for sexual reproduction, early spring for scouring and dispersal, and capsule production depending on whether it can take advantage of emergence or must disperse under water.

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